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How Marine Fishery Reserves Can Improve Reef Fisheries.

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ABSTRACT

Reef species are vulnerable to overfishing because of their life history characteristics. Various fisheries for reef species have declined worldwide, including the Caribbean, Gulf of Mexico, and U.S. south Atlantic. Traditional fishery management techniques may not be practical or effectively deal with certain problems, such as bycatch and release mortality. Marine fishery reserves, areas with no consumptive usage, provide an alternative management approach with attractive attributes from a fishery perspective. Marine fishery reserves can improve reef fish fisheries by protecting species composition, population age structure, spawning potential, and genetic variability within species. Reproductive output from reserves would help resupply fished areas by natural egg and larval dispersal. Properly located reserves of adequate size could protect the quantity and quality of reproductive output, reduce recruitment uncertainty due to environmental variation, and ensure against management failure. Marine fishery reserves are currently being used by several countries. Substantial empirical evidence shows that protection from fishing has increased fish abundance and availability inside and outside protected areas. The potential benefits of reserves appear to outweigh detriments for reef fisheries. A model of the red snapper *(Lutjanus campechanus)* fishery in the Gulf of Mexico with 20% of the habitat protected by reserves, showed that total egg production was potentially 1200% greater than under the status quo. The projected increased fecundity and subsequent fish availability would more than compensate the projected 25% greater fishing effort caused by displaced fishermen moving to open areas. Uncertainties remain concerning the ideal number, location, and size of reserves necessary to achieve management objectives.

INTRODUCTION

Reef fisheries commonly exploit a diverse assemblage of organisms including lobster, conch, corals, sponges, and fishes. Lobster and reef fishes in particular are popular fishery targets because they often achieve large size, have high market value, are accessible near coastal areas, and can be caught by a variety of fishing gears including spears, nets, traps, and hooks. Increasingly, it is being recognized that reef systems have limited fisheries production capacity and are easily overfished. Many reef species have been overexploited or show signs of being overfished in the Caribbean region and around the world (Pauly, 1979; Munro, 1983; Appeldoorn and Lindeman, 1985; Munro and Williams, 1985; Bannerot et al., 1987; Goodyear, 1989; Richards and Bohnsack, 1990).

The purpose of this paper is to review, from a fisheries perspective, the potential of marine fishery reserves (MFRs) as a management option for maintaining or enhancing reef fisheries. Marine fishery reserves, defined as areas with no consumptive usage, are increasingly being proposed and used to manage reef resources (Davis and Dodrill, 1980; Davis, 1989; PDT, 1990). This review is necessary because the fishery reserve concept is relatively new to marine fisheries and differs in many ways from more traditional management approaches. Any change in fisheries management is a justifiable concern for fishery interests and often brings automatic resistance. Thus, it is important to understand why MFRs are being proposed, how they are intended to work, and what are the expected benefits, problems, and limitations of their use. A better understanding of the issues should lead to more enlightened and productive discussions between those involved in fisheries research, conservation, and management.

With these objectives in mind, I reviewed information on the use and potential of marine protected areas for reef fishery management, emphasizing application for the Caribbean, Gulf of Mexico, and central western Atlantic, although other examples were used when appropriate. The major questions addressed were whether closed area reserves were necessary and effective, would pulse fishing accomplish the same objectives, and what were the tradeoffs, problems, and potential benefits of fishery reserves? Issues not directly related to fisheries use, although important, are not treated here (see IUCN, 1985; Lien and Graham, 1985; Van't Hof, 1985; Foster and Lemay, 1989; Ballantine, 1989; PDT, 1990; Batisse, 1990).

MAJOR ISSUES

Marine Protected Areas

Marine protected areas are commonly used worldwide for a variety of purposes and almost all allow at least some fishing (IUCN, 1985; Foster and Lemay, 1989). Many favor certain kinds of fishing activities, such as recreational or artisanal fishing, over others by excluding fishing methods considered destructive or unacceptable, such as explosives, trawls, or fish traps. In the U.S. Marine Sanctuary Program, for example, fish traps and spearfishing are excluded within Looe Key and Key Largo National Marine Sanctuaries, while other recreational and commercial fishing activities are permitted (Wells, 1988; Clark, *et al.*, 1989).

Marine fishery reserves that exclude all fishing and other consumptive uses are a relatively recent and rare occurrence, but are increasingly being recommended and used for reef resource management. Reserves have been used in Kenya, since 1968 (McClanahan and Shafir, 1990), in Australia and New Zealand since the middle 1970's (Kelleher and Kenchington, 1982; Ballantine, 1989), and in Bermuda beginning in 1990. They have been recommended for use in the U.S. and the Caribbean (Davis, 1989; Bohnsack *et al.*, 1989; PDT 1990, Richards and Bohnsack, 1990). Although some countries have declared reserve areas, compliance and their effectiveness is unknown because of little or no enforcement and monitoring.

Life History

Basic knowledge of the life history and ecology of typical reef organisms facilitates an understanding of reef fishery problems. Most reef species disperse as pelagic eggs or larvae via ocean currents. Before settling into bottom habitats they spend anywhere from a week to many months in the plankton depending on the species and location. Some reef species settle into nursery habitats, such as sea grasses and estuaries, or use non-reef habitats before moving onto reefs at older stages. However, once they arrive at a reef, most reef organisms tend to show strong site fidelity and limited geographic movement (Beinssen, 1988; PDT, 1990; Sale, 1980). Many reef organisms grow slowly, face low natural mortality, achieve large size, and are capable of living many years. Examples of potential ages among exploited species include 40 yr for jewfish, Epinephelus itajara, (GMFMC, 1990), 30 yr for red grouper, *Epinephelus morio*, (Jory and Iversen, 1989); 20 yr for red snapper, (PDT, 1990); 17 yr for red hind, *Epinephelus guttatus*, (Sadovy and Figuerola, in press); and over 20 yr for spiny lobster (extrapolated from Hunt and Lyons, 1986). Many exploited reef fishes change sex, usually switching from female to male as they get larger or older (Bannerot, *et al.*, 1987).

Juveniles put most of their energy into growth and survival, often delaying reproduction for several years. Most adults devote much of their energy to reproduction. Fecundity increases greatly with size for many reef organisms. For example, one red snapper at 61 cm total length has the same gonad weight as 212 females at 42 cm (Grimes, 1987). Thus, a few older organisms may be more important to total reproductive output than many younger ones during any given year. Also, reproductive success may be increased because of greater experience and knowledge of where and when to find mates.

The recent general scientific consensus is that the amount of adult habitat rarely limits the abundance of most reef populations except in cases of extreme habitat scarcity (Bohnsack, 1989). Many reef species appear limited by recruitment, showing high recruitment variability with exceptionally good and bad recruitment episodes (Doherty and Williams, 1988; Hughes, 1990). From an ecological perspective, reef fish life history characteristics may be considered as adaptations for recruitment uncertainty; long reproductive lives insure that fishes will be replaced in the next generation (e.g., "the storage effect"; Chesson, 1983).

A poor relationship usually exists between stock size and recruitment success. High levels of stock abundance and reproductive output do not necessarily result in good recruitment (Underwood and Fairweather, 1989). However, the probability of good recruitment drops with low population size and low reproductive output (Goodyear, 1989) and increases when adequate spawning potential is maintained. Without an adequate supply of eggs, excellent conditions for recruitment success can be wasted. This can be the case in heavily fished situations where the removal of the larger, older individuals by fishing activities has greatly reduced the effective reproductive output (Bohnsack, 1989; Polovina and Sakai, 1989).

More extensive reviews of life history and ecology are provided elsewhere for corals (Connell, 1973; Glynn, 1973), lobsters (Lyons, 1986; Herrnkind and Butler, 1986; Butler and Herrnkind, in press), and fishes (Sale, 1980; Munró, 1983; Munro and Williams, 1985; Doherty and Williams, 1988).

Fisheries Management

Fishing tends to deplete larger and older fish because larger fish have greater sport and economic value, are targeted by size selective fishing gear, and are often more vulnerable to fishing gears because of their aggressive behavior (Thompson and Munro, 1974; Nelson and Soulé, 1987). Fishing mortality on reef fishes is frequently greater than natural mortality (Table 1).

Fishery management strategies must consider characteristics of organisms that make them vulnerable to overfishing: slow growth, long potential lives, low natural adult mortality, strong site attachment, limited or predictable adult movements, high recruitment variability, first reproduction postponed to later ages, increased fecundity with age, and hermaphroditism. For example excessive size selective exploitation of hermaphroditic species could result in too few males to adequately fertilize eggs (Bannerot *et al.*, 1987).

The traditional biological objectives of fisheries management are to prevent growth and recruitment overfishing. Growth overfishing occurs when fish are taken before they have had a chance to grow. Management for growth overfishing seeks to maximize the yield from fish entering the fishery. Most frequently size limits and gear restrictions (e.g., mesh sizes, hook sizes) are used to prevent undersized fish from being caught.

Recruitment overfishing is more serious and occurs when fishing reduces adult stocks such that lower egg production increases the chance of recruitment failure. This can happen either by removing large numbers of young individuals (i.e., growth overfishing) or by excessive removal of larger

Table 1. Reported ratios of fishing mortality (F) to natural mortality (M) in the Caribbean region. Modified from Ralston (1987, Table 8.2)

Species	F/M	Location	Source
Snapper (Lutjanidae)			
Lutjanus campechanus	1.17 - 1.34	Carolinas	Nelson and Manooch (1982)
	1.63	East Florida	Nelson and Manooch (1982)
	1.21 - 1.32	West Florida	Nelson and Manooch (1982)
	2.90 - 3.70	Louisiana	Nelson and Manooch (1982)
	1.70	U.S Gulf of Mexico	Goodyear (1988)
	3.85	Age 3 fish, Gulf of Mexico	Goodyear (1990)
	2.00	Ages 5 - 9 fish, Gulf of Mexico	Goodyear (1990)
Lutjanus purpureus	1.66	Brasil	Ivo and Gesteira (1974)
	1.73 - 2.23	Brasil	Ivo and Hanson (1982)
Grouper (Serranidae)			
Centropristis striata	1.00 - 1.77	U.S. South Atlantic	Low (1981)
Epinephelus drummondhayi	0.35 - 0.85	U.S. South Atlantic	Matheson and Huntsman (1974)
Epinephelus guttatus	0.28	Jamaica	Thompson and Munro (1974)
Epinephelus niveatus	0.27 - 1.80	Carolinas	Matheson (1982)
Epinephelus striatus	2.52	U.S. Virgin Islands	Olson and LaPlace (1979)
Mycteroperca microlepis	3.00	West Florida	McErlean (1963)
Mycteroperca phenax	1.24	Carolinas	Matheson, et al. (1984)
Tilefishes (Malacanthidae)			
Lopholatilus chamaeleonticeps	3.0 , 5.6	U.S. South Atlantic	Mightower and Grossman (1988)

reproductive individuals. Management for recruitment overfishing seeks to ensure an adequate resupply of new fishes (recruits) to the population by lowering fishing mortality and increasing adult survival. Management strategies can include size limits, bag limits, quotas, limited entry, fishing seasons, gear restrictions, and area closures (Munro and Williams, 1985).

The spawning potential ratio (SPR) is an index used to warn of potential recruitment overfishing and is based on the biological ability of the adult fish to produce spawn or eggs (Goodyear, 1989). SPR is defined as the spawning ability of the species when being fished divided by the spawning ability under natural conditions with no fishing. The chances of recruitment failure increase greatly at low SPR values. Although variable by species, a 20% SPR is frequently used as a rough first approximation of a critical minimum level until empirically derived information can be obtained.

Many traditional management approaches can fail because of high release mortality, high fishing pressure, or unenforceable regulations. Some management approaches demand continuous and intensive data which are sometimes difficult to obtain and vulnerable to cheating or misrepresentation. Data collection often depends on good will by those involved in the fishery. Monitoring reef fisheries and stocks may be impractical because of the large number of fishing operations, the number of species in the fishery, and the different kinds of fishing gears used.

Marine Fishery Reserves

Recent theoretical and applied studies suggest that marine fishery reserves may benefit reef fisheries and could treat many of the problems associated with traditional management approaches (Davis, 1989; PDT 1990). No fishing zones are primarily intended to prevent recruitment overfishing by maintaining sufficient spawning stock and to provide an adequate supply of recruits to surrounding fished areas (Figure 1). They work by taking advantage of the natural life history features of most reef organisms, especially the fact that most post-settlement reef fishes are rather sedentary and strongly site specific. Fishes protected from harvesting within reserves are allowed to mature and achieve a natural age distribution so that larger and older individuals, which supply the majority of eggs, are able to reproduce. The natural dispersal of eggs and larvae by ocean currents will help resupply recruits both to reserves and surrounding fished areas.

Most traditional management techniques seek to protect spawning stock by establishing a numerical refuge based on population size. Quotas, bag limits, size limits, and gear restrictions, for example, are intended to maintain stocks by allowing a sufficient number of fish to escape harvest in order to reproduce.

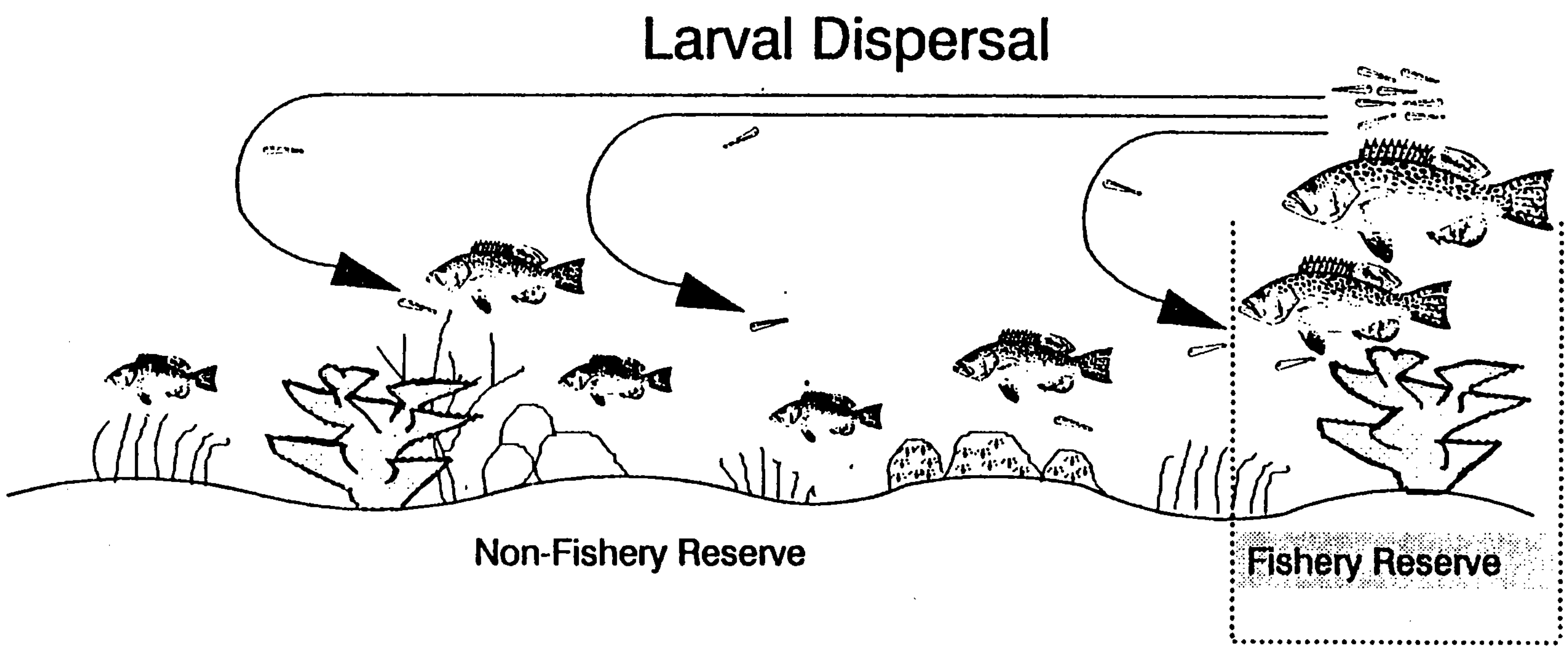

Figure 1. Dispersal of offspring using fishery reserves. Adult stocks are protected from harvesting inside reserve areas while their eggs and larvae are dispersed to reserve and fished areas by natural processes.

Management using MFR's seeks to do the same thing by providing a population refuge in space instead of a refuge in numbers. It becomes a preferable alternative when traditional approaches don't work, when it is more economical to enforce, or when adults show strong site fidelity.

Until recently, most reef fisheries have probably been partially maintained by defacto refugia-- areas too deep, too remote, or too difficult to easily locate. The effectiveness of these refugia has greatly diminished with improved fishing and navigation methods and with increased human demand. Some obvious examples of improved technology impacting fisheries include inexpensive engines, LORAN, SCUBA, synthetic fishing lines, bottom long-lines, depth sounders, and improved weather forecasting.

Substantial evidence shows that areas receiving total or partial protection from fishing have increased fish abundance or availability (Randall, 1982; White, 1986, 1988; Ballantine, 1989; Davis, 1989). For example, spiny lobster (Panulirus argus) abundance was much greater in areas completely protected from recreational harvest than in unprotected areas of the Dry Tortugas, Florida, U.S.A. (Davis, 1977). After 10 yr of protection, numbers of rock lobster (Jasus edwardsii) were very much higher in the Cape Rodney to Okakari Point Marine Reserve, New Zealand, (Cole, *et al.*, 1990). Densities of exploited reef fishes have been shown to be much higher at reefs protected from spearfishing in the Florida Keys, U.S.A. (Bohnsack, 1982; Clark *et al*, 1989; PDT 1990). Increased abundance and size of some fishes has been shown from areas protected from all fishing activities off Kenya (McClanahan and Muthiga, 1988; McClanahan and Shafir, 1990) and New Zealand (Ballantine, 1989; Cole, *et al.*, 1990). At Bolt Reef, Australia, a significant replenishment of commercially important fish stocks was observed after a 3.5 yr fishing closure (Beinssen, 1988). Similar changes have been noted at Hanauma Bay, Hawaii which has been protected from all fishing since 1967 (Billig, 1990). A reserve at Sumilon Reef, Philippines not only had a greater abundance of exploited fishes but was also credited with maintaining fisheries in surrounding areas by exporting biomass to the non-reserve areas (Alcala, 1988; Alcala and Russ, 1990).

To better understand the potential effects of marine reserves, I modeled survival (Figure 2) and fecundity (Figure 3) of a cohort of 10,000 female red snapper (Lutjanus campechanus) using growth and age-specific mortality estimates from the Gulf of Mexico between 1984 and 1988 (Goodyear and Phares, 1990). Annual measured fishing mortality was 0.002, 0.0208, 0.2956, 0.7736, 0.5608, 0.4006, 0.3782, 0.4118, 0.4714, 0.4426 for year classes 0 to 9, respectively, and 0.5308 for years 10 and above (see Table 35 in Goodyear and Phares, 1990). Annual natural mortality was assumed to be 0.20. Fecundity estimates were based on gonad weight and estimated from average

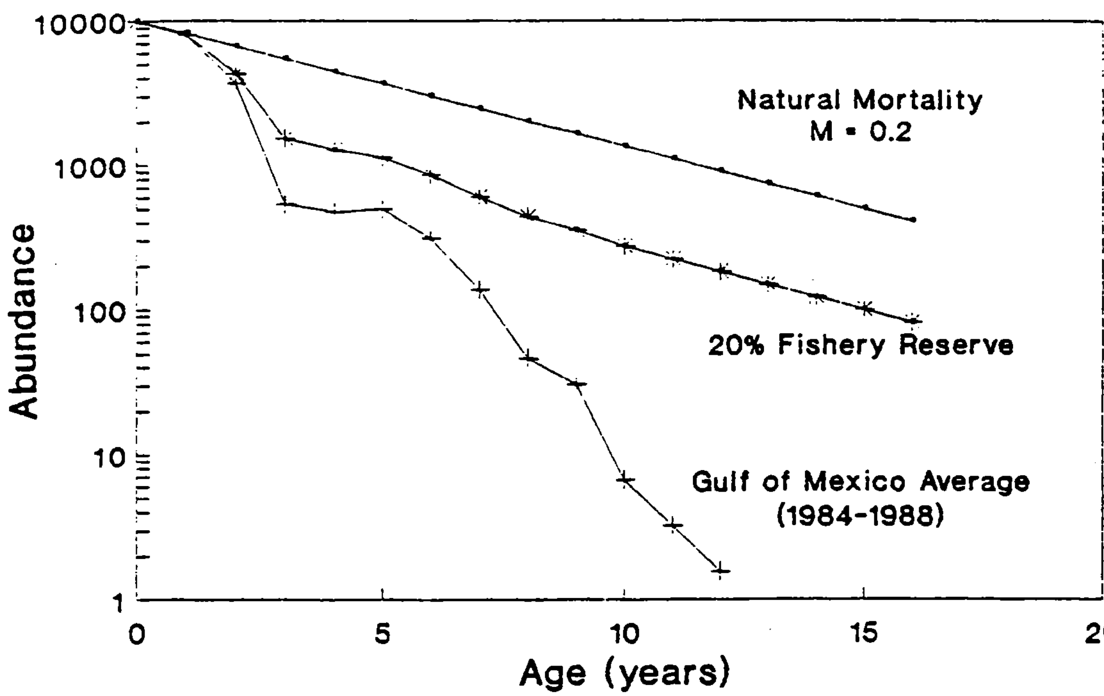

Figure 2. Estimated survival of a cohort of 10,000 red snapper under conditions of natural mortality, average fishing mortality observed in the Gulf of Mexico between 1984 and 1988, and under conditions of a simulated reserve system that protects 20% of the population. The reserve system assumes 20% of the cohort experiences only natural mortality while the remaining 80% experiences the above fishing conditions. See text for details.

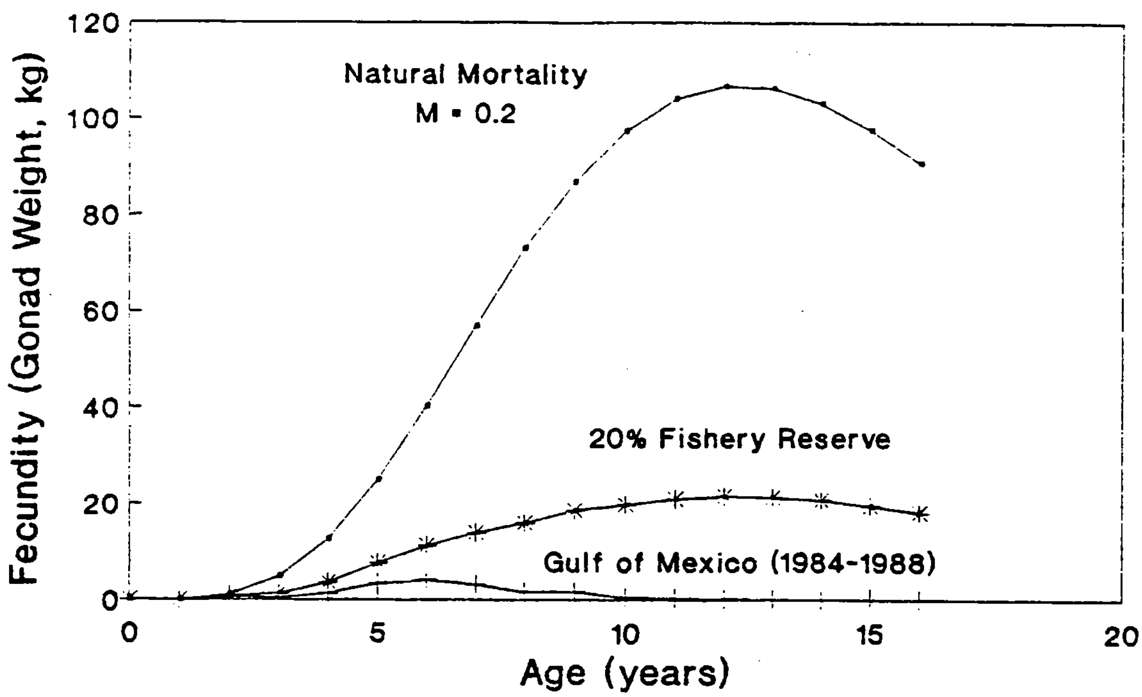

Figure 3. Estimated red snapper total fecundity (gonad weight) under conditions of natural mortality, average fishing mortality observed in the Gulf of Mexico between 1984 and 1988, and under conditions of a simulated reserve system that protects 20% of the population. The reserve system assumes 20% of the cohort experiences only natural mortality while the remaining 80% experiences the above fishing conditions. Fecundity is based on a cohort of 10,000 fish and abundances shown in Figure 2. See text for details.

length-at-age using equations provided by Goodyear (1988):

$$\ln(gw) = -16.1 + 5.87^{\ln(L)}$$

$$L = 45.9(1\text{-}\exp(-0.115(age+0.50)))$$

where gw is gonad weight in grams, L is total length in inches, and age is in years.

In the model a total of 20% of the habitat was protected by fishery reserves while the remaining 80% of the habitat outside of reserves experienced normal fishing mortality. For simplicity the model assumes no fish movement so that protecting 20% of the habitat from all fishing activity protects 20% of the stock. In reality, the amount of area needed to protect 20% of the stock would vary depending on fishing effort, home range size of red snapper, and the actual number, size, shape, and location of reserves. I chose to protect 20% of the stock based on the critical minimum spawning potential ratio discussed earlier. To be conservative, several factors were not considered that would have increased the apparent benefits of reserves. Bycatch mortality from shrimping was not considered which would have increased fishing mortality estimates. Only one reproductive event was assumed per year even though larger females may spawn more than once (Grimes, 1987). Also, no fecundity was provided for fishes over age 16 (assuming some senescence) although it is probable that some fecundity is provided older individuals (Grimes, 1987).

The projected effects of fishing reserves are shown for abundance (Figure 2) and fecundity (Figure 3). Reserves guarantee that total abundance and fecundity would be at least 20% of what would occur under natural conditions. For example, approximately 1353 fish would survive to reach age 10 under natural conditions, 276 fish would survive with the reserve option, but only 7 would survive under average fishing effort in the Gulf of Mexico. The total SPR with reserves was 21.43%. Total fecundity (gonad weight) from the unfished stock was 1008 g per female. With 20% of the stock protected by reserves, total fecundity was 216 g per fish, approximately 1200% greater than the 18 g that would occur if all areas experienced normal fishing activity (Figure 3).

When stocks are well below their potential natural abundance, it is reasonable to assume that the total supply of fish is directly related to total egg production (Goodyear, 1989). Assuming good dispersal of eggs and a direct relationship between egg production and the supply of fish, there would be far more fish available to fishermen with reserves than without them. This occurs even though areas open to fishing would receive greater fishing pressure caused by fishermen displaced from protected reserve areas. If 20% of the habitat was closed to fishing, then 20% of fishing activities could be transferred to the remaining 80% of the habitat open to fishing. This would result in a 25% increase in effort for the available fishing area (i.e., 100% fishing effort / 80% area = 125% fishing effort / area). Thus, total fish production must increase more than 25% to compensate for the lost fishing area. Using this model, a 1200% greater supply of eggs should more than compensate fishermen displaced from closed fishing areas.

Pulse Fishing

One frequently suggested variation of fishery reserves is to periodically open up reserves to fishing (pulse fishing). Based on theoretical grounds and available data, this approach is probably not very workable for reef species. The closure period would likely have to be considerable given that most harvested reef organisms have a life cycle that lasts for many years. Determining the length of time between pulses would be difficult because reef fisheries include many species, each having different optimal pulse periodicities. Also, pulse fishing is primarily directed at increasing yield per recruit, it is less well suited for increasing reproductive output. Finally, at least three studies described below have shown that pulse fishing rapidly depleted reef stocks which took years to rebuild.

A pulse fishing experiment was done using an unfished population of spiny lobster in the Dry Tortugas, Florida (Davis, 1977; Davis and Dodrill, 1980). Half of an area closed to fishing was opened to fishing by recreational divers who were limited to 2 hand caught lobster per person per day. The other half remained an unfished control area. After one season (8 mo), total catch rates were reduced 58% from pre-harvest levels in the opened area while catch from the control area was unchanged. The decline is remarkable in the speed with which it occurred despite the probable low level of harvest due to the remoteness of the study site from human population centers.

A tagging experiment at Boult Reef, Australia also showed that the benefits of closing an area to all fishing can be rapidly dissipated by renewed fishing (Beinssen, 1988). Boult Reef, approximately 3.5 x 2 km, was designated a "replenishment area" and closed to all fishing for 3.5 years (1 July 1983 and 1 December 1986). In the two weeks following the re-opening of the reef to fishing, 25% of the estimated grouper population (approximately 2000 grouper) were caught in about 1200 man-hours of recreational fishing.

In an unplanned experiment, a 26% drop in total fish abundance and a 94% decline in Lutjanids (snappers) and Lethrinids (emperors) occurred within 18 months of relaxed protection at Sumilon Reef in the Philippines (Alcala, 1988; Clark *et al.*, 1989; Russ and Alcala, 1989). Although this reserve was effective for approximately 10 years, management collapsed in 1984 and was followed by extensive fishing in the former reserve areas. After the reserve collapsed total fish landings at Sumilon Island declined 54% within 2 years (Alcala and Russ, 1990).

DISCUSSION

Tradeoffs

The tradeoffs between potential gains and losses is a major concern for fishermen. In order to achieve gains, something must be given up. Unfortunately the threat of a loss often has more potential psychological impact than the possibility of gains (Kahneman and Tversky, 1982). Some important fisheries tradeoffs are discussed below.

Detrimental Considerations

1. Potential harvest is lost from areas permanently closed to fishing. This loss will be approximately proportional to the areas included in reserves. Over the long term, reserves compensate for lost fishing area by increasing total production from areas open to fishing.

2. A time lag will exist between closure and the onset of full benefits of a reserve. Increased recruitment depends on the growth rates of each species, the number of fishes already in reserve areas, and on subsequent recruitment. In general, the more severe the overfishing before reserves are established, the longer it will take for the full benefits to be achieved because there is less chance of good recruitment and smaller stock available to grow and increase the spawning potential.

3. Fishermen near reserves will have to travel greater distances to fish. This effect will vary between areas depending on the location and size of reserve areas. Most fishermen would not be directly effected.

4. Areas open to fishing would receive increased fishing pressure caused by fishermen displaced from areas protected by reserves. As discussed earlier, the increased supply of fish should more than compensate for this displacement.

5. Reserves are unlikely to benefit highly migratory species. For these species, the expected benefits of reserves would be in proportion to the length of time an individual fish remained in the protected area. Benefits of reserves could easily be dissipated by increased fishing effort outside reserve areas. Temporary seasonal closures may be helpful for migratory species with predictable movements. Bermuda has dealt with this problem by establishing seasonally closed areas as well as permanently closed areas to protect

spawning aggregations (James Burnett-Herkes, pers. comm., Division of Fisheries, Bermuda).

Beneficial Considerations

Fishery reserves offer several major and many secondary benefits to reef fisheries:

1. The total potential harvest should be maximized by ensuring adequate egg production and supply of recruits. Total harvest will increase for species previously overfished. Again, the red snapper model with 20% habitat reserve, predicts 1200% greater total fecundity than that under fishing mortality in the Gulf of Mexico between 1984 - 1988 (Figure 3).

2. Reserves can reduce recruitment uncertainty from natural environmental variation. A major concern is that fishing mortality can reduce the average age structure of a population so that only a few breeding year classes produce most of the reproductive output. Several years of poor recruitment due to natural events could collapse a stock when fishing mortality has severely reduced the breeding stock (PDT, 1990). For example, Goodyear and Phares (1990) noted that the Gulf of Mexico red snapper fishery was being maintained by a few year classes. Continued fishing mortality on these year classes combined with several years of poor recruitment could collapse the fishery. A reservoir of protected breeding stock in reserve areas would maintain the reproductive output.

3. Reserves would provide some protection against management failure by reducing the risks of traditional fishery management approaches. All fishery management has some uncertainty and degree of risk. However, fishery reserves can act as a reservoir to rebuild stocks when traditional fishery management regulations fail and may buffer against ecosystem disruption due to excessive fish removal.

4. Reserves can protect the genetic integrity of the species from detrimental fisheries selection. Unlike animal husbandry, fishing harvests wild populations and may remove individuals with the most desirable characteristics from the breeding population. Population characteristics most desirable to the fishery, such as large body size, may be reduced over time from intense fishing mortality (PDT, 1990). Recruits of many reef species currently have a better chance of dying by fishing than by natural causes (Table 1). Reserves can protect those genetic characteristics by allowing natural selective processes to work in reserves where large body size or delayed reproduction is still an advantage.

5. Reserves can provide better data on natural mortality thereby improving fisheries by reducing assessment uncertainties and providing more precise and accurate predictions. Fishery models depend greatly on estimated natural

mortality which are essentially impossible to measure with precision in a fished population. Fishery models could be improved by allowing independent measurements to be obtained from reserve areas.

6. One desirable feature of fishery reserves is that treatment would be equitable among fisheries. Because all fishing is prohibited, one fishing gear or group would not be favored over another.

7. With a reserve system, a higher total amount of fishing activity may be possible than would be otherwise possible for a given level of spawning potential. Restrictions could be less severe and allow more fishing activity in fished areas because of the spawning stock protected in reserves.

8. The reserve approach may provide a viable strategy for cooperative management of international fisheries. Coordinated regional management is often desirable because efforts by individual countries may not be effective. Caribbean reef fish populations are most likely interconnected through egg and larval dispersal; stocks in one area may depend on recruitment from upstream sources. Thus, some countries may deplete their stocks with little impact on local recruitment. This situation provides little incentive for local conservation because population resupply will continue from upstream sources, even though downstream recruitment may suffer. Eventually however, increased population demands and expansion of fishing effort are likely to exploit remaining source stocks, threatening their regional persistence. Coordination is difficult because the Caribbean is divided geographically and politically into at least 38 countries or territories with different cultures and varying levels of public education and economic development (Richards and Bohnsack, 1990). With the reserve approach each country could contribute reserves in proportion to its shelf area and potential biotic wealth.

9. Reserves should reduce conflicts between fishing interests and non-consumptive users. Environmental, conservation, research, and educational needs could be accommodated within reserves without conflict with fisheries. Some activities could continue or be enhanced in reserve areas, such as tourist diving, underwater photography, and behavioral and ecological research.

10. Fishery reserves could improve overfished fisheries and increase the supply of fish by addressing the following problems that are often not adequately treated by traditional management approaches:

(A) Overfished species are incidentally caught and killed even when at low densities because most reef fisheries harvest many species using non-selective reef fishing techniques.. Within reserves this incidental harvest is eliminated so that the abundance of these species is set by natural limits.

(B) High bycatch or release mortality associated with many fishing methods is eliminated within reserves because there is no fishing of any kind. For example, millions of juvenile red snapper are killed in shrimp trawls and many undersized fish caught by recreational fishermen may die when released (Goodyear and Phares 1990).

(C) Many traditionally used regulations are difficult to enforce or compliance is difficult to monitor. In some cases, compliance may be better with reserves than with traditional methods because enforcement and educational effort can be focused in a limited area and violations may be more easily detected.

(D) A major problem in traditional management approaches is that fishing selectively removes larger and faster growing individuals which over time may genetically alter the species in undesirable ways from a human perspective (Davis and Dodrill, 1980; Bergh and Getz, 1989; PDT, 1990). The major concerns are that fishes will tend to become precocious (i.e., mature early and reproduce at small sizes) and adults will become diminutive in size as has been experimentally demonstrated for stream fishes in Trinidad (Reznick and Endler, 1982). Reproduction at smaller sizes generally means lower total reproductive output, which combined with smaller populations sizes due to fishing mortality, makes the population more vulnerable to recruitment failure by natural environmental variation. Within reserves fishes with genes for large size and rapid growth can maintain their natural advantages by being protected from fisheries selection. These individuals can resupply offspring with those traits to the general reef fishery. The red snapper model showed that individuals within reserves could account for a significant portion of total eggs produced compared to output from fished areas under current levels of fishing effort (Figure 3).

(E) Fishermen can locate and remove fish even when stocks have been severely depleted because reef habitat is limited in space and fish movements are predictable in time. The widespread use of LORAN for navigation simplifies the location of remote or difficult to find reefs. Also, some reef species make predictable migrations to spawning areas where they are easily fished. This spatial and temporal predictability can be treated by including critical areas within reserves.

Unresolved Issues

Some scientific uncertainties exist concerning the number, size, and specific locations best suited for reserves. The International Union for the Conservation on Nature and Natural Resources (ICUN) has set a goal of protecting at least one-third of all coastal seascapes (Batisse, 1990). The South Atlantic Fishery Management Council Snapper-Grouper Plan Development Team recommended protecting 20% of the habitat based on theoretical considerations about spawning stock biomass (PDT, 1990). The Sumilon Island reserve in the central Philippines protected approximately 25% of the sub-tidal coral reef from all forms of exploitation and was credited with helping to maintain high fishery yields in surrounding areas (Alcala and Russ, 1990).

The specific sites, sizes, and number of reserves necessary to protect stocks could be affected by a variety of local factors which are difficult to evaluate until a reserve is in place. To to be effective, reserves should probably include nursery areas and non-reef habitats. Most research on refuges has been applied to terrestrial reserves and few empirical data exist to evaluate ideal reserve size for most marine organisms.

Considerable discussion has occurred among conservation scientists concerning the relative benefits of having a few large or many small reserves. This has become known as the SLOSS (Single Large Or Several Small) problem. Soulé and Simberloff (1986) concluded that there is no general answer as to how large and how many are sufficient although they should be as large as possible and there should be many. In a recent review, Simberloff (1988) concluded that although most refuges tended to be too small, especially for large species, there was no biological reason for pessimism in using refuges especially with a metapopulation structure (a population structured as subpopulations in discrete areas with some interchange).

An effective reserve should have a sufficient population size to be reproductively active. The area needed would most likely be based on the home range size of species needing protection. Obviously the area included within reserves must be large enough to keep residents from being captured outside reserve areas during their normal movements. It is possible that small strategically located areas could be protected and be effective. Pulliam (1988) developed the concept of "sources and sinks" in which source areas are net exporters of individuals, while sink areas are net recipient areas in which within-habitat reproduction is insufficient to balance local mortality. Ideally source areas would be the most beneficial as reserves.

Obviously, a number of social and economic factors beyond the scope of this review are also important to consider when designating reserve areas. Ideally, fishermen should be involved in selecting sites so the reserves are least disruptive but effective for fisheries improvement. Site selection, although difficult and potentially contentious, would benefit greatly from the experience and local knowledge only available to fishermen. The experience in New Zealand suggests that despite initial opposition to a reserve, 78% of the fishermen eventually favored having additional reserve areas (Ballantine, 1989). Also, 40% of the fishermen considered their catches were now higher outside the reserves than before reserves were established. The 40% figure is significant considering that only 40% of the fishermen had been fishing long enough to personally know the situation before reserves were in place (10 years). Ballantine (1989) concluded that social and political problems of creating reserves were much larger in prospective imagination than in actual practice.

Limitations

Although MFR's are intended to improve reef fisheries, they will not solve all fishery problems and other management actions will still be necessary to maximize the yield from fished areas. Like any management approach, MFR's will bring their own sets of problems. Clearly, the expense of public education and compliance enforcement is an important consideration; however, protecting limited reserve areas may be more cost effective than attempting to educate and enforce a variety of regulations over large areas. Even if fish stocks are increased, reserves by themselves will not solve problems of habitat destruction and pollution nor competitive conflicts between different fisheries or user groups (e.g., recreational versus commercial, line versus trap fishing). No matter how effective reserves are, fishing effort will have to be adjusted to natural biological limits on reef productivity. Despite these limitations, fishery reserves still offer great potential benefits for reef fisheries in the Caribbean and elsewhere.

CONCLUSIONS

Reef resources are vulnerable to overfishing and have been overfished in many places. Traditional fishery management techniques may not be practical or effectively deal with some problems such as bycatch and release mortality. Marine fishery reserves provide an alternative management approach with attractive attributes from a fishery perspective. Properly located reserves of adequate size could protect the quantity and quality of reproductive output, reduce recruitment uncertainty due to environmental variation, and ensure against management failure. Substantial evidence shows that total or partial protection from fishing has increased fish abundance and availability inside and outside protected areas.

The major problems of using reserves are determining which sites and how much area to include as reserves. Although stock abundance has been shown to increase in protected areas, scientific uncertainties remain concerning the proper size, number, and exact location of reserves to achieve management goals. A lag time is expected before full benefits of increased spawning stock take place. Also, the displacement of fishing activities from reserve areas will have to be addressed. Several studies have shown that stocks were rapidly depleted when protected areas were opened to fishing activities.

The potential benefits of reserves appear to outweigh detriments for reef fisheries. The red snapper model with 20% of the habitat protected by reserves showed that total egg production was potentially 1200% greater than the status quo and that total fish supply should improve even though areas open to fishing would be expected to receive 25% more fishing effort. This seems like a reasonable tradeoff although the actual effects of reserves would vary among species. Certainly losing 20% of the fishing area seems

to be a more attractive alternative than a fishery collapse or the necessity of total closure to rebuild depleted stocks. Total closure has occurred in U.S. federal waters for red drum and jewfish and is being considered for red snapper, Nassau grouper, and other reef species. Giving up a portion of the fishing area seems preferable to a collapsed or totally closed fishery especially if yield can be increased.

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